

The phylogenetic relationships of the Elasmotherini (Rhinocerotidae, Mamm.)

By MIKAEL FORTELIUS and KURT HEISSIG^{*)}

With 2 figures

Abstract

A cladistic analysis of the extinct rhinoceros tribe Elasmotherini is presented, based mainly on dental morphology. The result is a new classification of *Begertherium* (formerly *Hispanotherium*) *grimmi* (HEISSIG) and *Begertherium* (formerly *Beliajevina*) *tekkayai* (HEISSIG). It is possible to recognize a *Hispanotherium*-clade and an *Elasmotherium*-clade at a suprageneric level, but to do so formally serves no useful purpose.

Kurzfassung

Die vorliegende cladistische Analyse des ausgestorbenen Nashorn-Tribus Elasmotherini stützt sich vor allem auf die Gebißmorphologie. Es ergibt sich eine neue systematische Zuordnung von *Begertherium* (früher *Hispanotherium*) *grimmi* (HEISSIG) und *Begertherium* (früher *Beliajevina*) *tekkayai* (HEISSIG). Es ist möglich, oberhalb der Gattungsebene einen *Hispanotherium*-Zweig und einen *Elasmotherium*-Zweig einander gegenüberzustellen. Es erscheint jedoch nicht zweckmäßig, daraus systematische Konsequenzen zu ziehen.

Introduction

The first attempt to establish the phylogenetic relationships of the different genera of Elasmotherini by HEISSIG (1974) was based mainly on the position of the horn, the degree of hypsodonty and the loss of incisors. We now consider these characters less significant than special features of the dentition, partly because the subsequently discovered *Ningxiatherium* is intermediate between *Iranotherium* and *Elasmotherium* in horn position and morphology of the zygomatic arch (CHEN 1977). Increased hypsodonty and incisor loss are subject to parallel evolution and so somewhat problematic, although reversals are highly unlikely. The material available is certainly very incomplete, and any scheme based on it must be considered preliminary. It is nevertheless possible, at this stage, to present a logical and useful phylogeny of this puzzling group.

^{*)} Dr. M. FORTELIUS, University of Helsinki, Dept. of Geology, Division of Geology and Paleontology, Snellmaninkatu 5, SF-00170 Helsinki, Finland. Prof. Dr. K. HEISSIG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Richard-Wagner-Str. 10, 8000 München 2, FRG.

Classification

Most authors (e. g. BREUNING 1924, CHOW 1958, THENIUS 1969) have treated the elasmotheres as a subfamily Elasmotheriinae of the family Rhinocerotidae. HEISSIG (1972) pointed out strong resemblances to the extant rhinoceroses, and reduced the elasmotheres to tribal rank of the subfamily Rhinocerotinae. GROVES (1983), however, divided the extant rhinoceroses into two tribes and argued for subfamilial ranking of the elasmotheres. In order not to inflate the number of rhinocerotid subfamilies we have kept the elasmotheres as tribe Elasmotherini, with the extant species classified at the subtribal level.

The Elasmotherini now comprise the following genera:

Elasmotherium FISCHER 1808

Sinotherium RINGSTRÖM 1923

Iranotherium RINGSTRÖM 1924 with the two species *I. morgani* de MECQUENEM 1908 and *I. mongoliense* OSBORN 1924

Hispanotherium CRUSAFONT & VILLALTA 1947

Begertherium BELIAJEVA 1971

Caementodon HEISSIG 1972

Kenyatherium AGUIRRE & GUERIN 1974

Beliajevina HEISSIG 1974

Ningxiatherium CHEN 1977

Tesselodon YAN 1979

In our opinion the supposed elasmotherine genus *Shennongtherium* HUANG & YAN 1983 belongs to the Rhinocerotini. *Kenyatherium* is excluded from the following analysis as it is based only on two upper premolars, not enough for useful comparison.

Characterization of the Elasmotherini

In the present classification, the Elasmotherini are the sistergroup of the Rhinocerotini (= Rhinocerotini + Dicerotini sensu GROVES). There are several shared characters: Strong median horn(s) [1], a long mandibular symphysis [2], a double rooted dp_1 [3], presence of rather strong and narrow metacone ribs in the upper premolars, weaker and broader in the molars [4], and a broad articulation of the ulna with the intermediate. The last two are plesiomorphic, and occur in tapiroids as well.

In most divergent characters the Elasmotherini are apomorphic with respect to the Rhinocerotini. The only autapomorphy of the extant rhinoceroses is the molarization of the upper premolars [5], while the elasmotheres as a group are plesiomorphic for this character. The basic elasmothere character complex includes the following elements: elongation of the metastyle of upper molars [6], a hypoconid demarcated buccally by distinct vertical grooves in the lower molars [8], a strong protocone constriction of the upper molars [7], the loss of the posterior articulation of radial and intermediate in the carpus [9] and a shortened collum astragali [10]. Characters [6] and [8] are unequivocal, but a constricted protocone has evolved in several rhinocerotid lineages, usually in association with other characters reflecting increased wear tolerance. The earliest known true rhinoceroses nevertheless exhibit a very weak distal protocone fold, in the manner of the extant species, so the strong constriction may be an autapomorphy of the Elasmotherini. The loss of posterior articulations in the carpus has also occurred several times within the family, always in combination with other changes towards increased cursoriality.

This is in marked contrast to the Rhinocerotini, in which an additional posterior articulation is developed between the ulnar and the intermediate.

History of the Elasmotherini

Most of the middle Miocene elasmotheres appear to be closely related. Given the nature of the available material they can be separated only on the basis of special traits of the dentition. Only a few specimens from the middle Miocene show similarities to upper Miocene and later forms. Two probable autapomorphies of the mainly middle Miocene *Hispanotherium*-clade are a short metaloph in the upper molars [11] and a strong pseudhypocone in the upper premolars [12]. The pseudhypocone in the p^{3-4} of the mainly stratigraphically later *Elasmotherium*-clade forms only a thin, angled wall [28]. It is probable that a pseudhypocone had not yet separated from the protocone at the time of divergence, in which case both conditions would be apomorphic. Shortening of the metaloph may also have occurred in the upper molars of some species of the *Elasmotherium*-clade. Premolar reduction [29] is highly characteristic of the *Elasmotherium*-clade, but is not seen in the *Hispanotherium*-clade. There is a general tendency for the metaloph of p^{3-4} to turn towards distolingual and straighten, changing its originally semilunar occlusal outline. This state seems to have evolved in parallel several times, including at the base of the *Elasmotherium*-clade [27].

One common character of the *Hispanotherium*-clade is the deep postfossette of the upper premolars. In *Caementodon* and *Hispanotherium* it has lost the lingual part and so the primitive semilunar shape, and has become triangular [13]. Both genera include the cingula in the increasing height of the crown [14]. They reach only a partial hypsodonty of the ectoloph [15]. In *Caementodon* the ribs of the ectoloph are flat [16]. *Hispanotherium* reaches larger size but remains morphologically more primitive.

The genus *Begertherium* forms another branch of this group. The ectoloph of upper teeth is not curved and the teeth are subhypsodont [18]. The premolars are at least as high as the molars [19]. This is one of the lineages where the incisors are lost, but a general tendency of incisor reduction is seen in the whole tribe. Even the most primitive forms had only small, triangular lower incisors and equally small, conical upper ones. Wear facets are evidence that these incisors were still functional, however. *Begertherium tekkayai* probably lacked incisors [21], whereas *B. borissiaki* and *B. grimmi* retained strongly reduced ones [20]. *Begertherium* had postfossettes of the primitive, semilunate shape. The mesial cingulum is high on the upper premolars but low on the molars, whereas the distal cingulum is high on both [23]. These characters unite the species *B. grimmi*, which was placed in *Hispanotherium* by HEISSIG (1974), with *B. borissiaki* BELIAJEVA 1971. *B. grimmi* is derived in the more frontal position of the horn [24] and the shorter nasals [25]. *B. tekkayai* is primitive in its more shallow postfossette, but advanced in its (probable) loss of incisors.

The *Elasmotherium*-clade

All the genera of this group seem to form simple side branches of one lineage, leading to the latest and most derived genus *Elasmotherium*. A major characteristic of the whole clade is the allometric increase of molar size, and corresponding premolar reduction. In *Beliajevina caucasica* (BORISSIAK 1935) the tooththrow retains plesiomorphic proportions. This is the most primitive member of the clade, with one single good apomorphy: the straight hypolophid of the lower

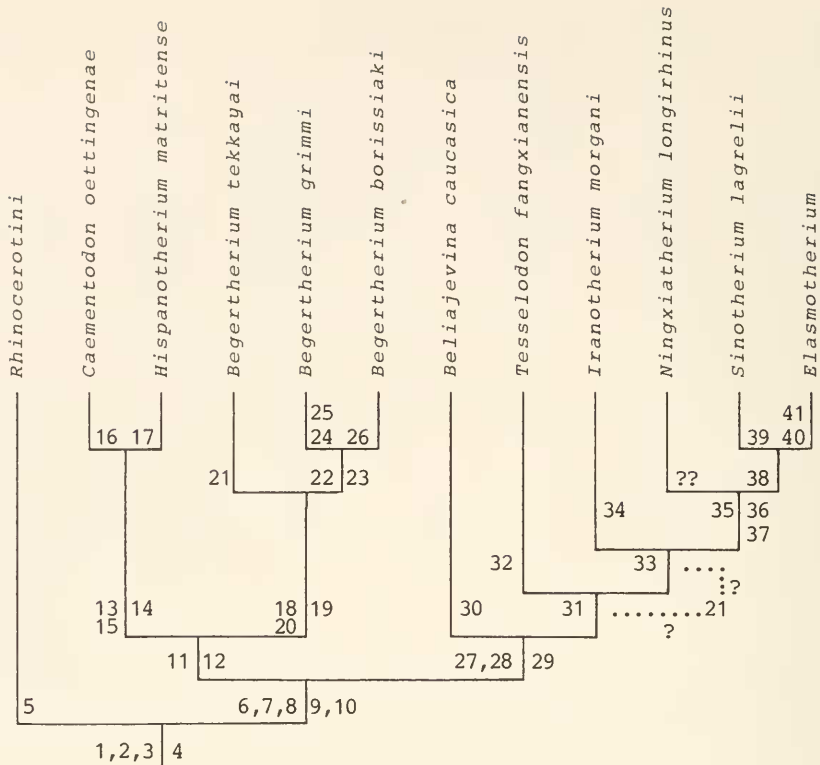


Fig. 1: Cladogram of the Elasmotheriini, with the Rhinocerotini (incl. Dicerotini) as outgroup.

Characters: 1. Strong median horn(s), 2. long mandibular symphysis, 3. double rooted P_1 , 4. rather strong metacone ribs in upper premolars, weaker ones in molars, 5. molarization of P^{3-4} to semi- or paramolariform stage, 6. metastyle of M^{1-2} elongate, 7. protocone of upper molars constricted, 8. hypoconid of lower molars conical, 9. posterior articulation of radial and intermediate lost, 10. collum astragali short, 11. metaloph of upper molars short, 12. pseudhyocone of upper premolars strong, 13. postfossette of upper premolars reduced lingually, deep labially, 14. cingula of upper teeth high, 15. partial hypsodonty, 16. outer wall of upper teeth curved, ribs flattened, 17. bigger size, 18. subhypsodont teeth, 19. upper molars equal in height with premolars, 20. incisors reduced, 21 (independently twice). incisors lost, 22. postfossette of upper premolars deep but still semilunate, 23. posterior cingulum of upper teeth high, anterior only in premolars, 24. horn shifted backwards, 25. nasals short, 26., ??, 27. metaloph of P^{3-4} directed backwards, 28. lingual posterior edge of the same teeth formed by a thin wall, 29. premolars reduced in size and height compared with molars, 30. hypolophid of lower molars nearly straight backwards, 31. metaloph of P^2 directed backwards, 32. ??, 33. deep groove between metacone and metastyle of upper molars, 34. very high zygomatic arch, 35. nasal notch retracted, 36. dentition shifted forward relative to cranium, 37. nasal septum ossified, 38. upper molars with strong crista, 39. ??, 40. upper premolars finally molarized, 41. cheek teeth rootless, evergrowing, prismatic.

molars, which in m_3 is hardly turned towards lingual at all [30]. The metaloph of p^2 is still directed towards lingual, in contrast to *Tesselodon* YAN 1979, which shares a backwards directed metaloph of p^2 with all later members of the clade [31]. *Tesselodon* is known only by its upper cheek dentition. Thus presence of incisors and shape of lower molars are indeterminate, and no autapomorphies are known.

The oldest form to show the characteristic skull modifications of this clade is *Iranotherium* RINGSTRÖM 1924. In the dentition it shares a deep vertical groove between metacone and meta-style of the upper molars [33] and incisors loss with later forms. The curiously inflated zygomatic arches with their hornbase-like pads rising high above the skull roof [34] constitute a striking autapomorphy of this genus. *Iranotherium* is similar to *Ningxiatherium* CHEN 1977 in the nasoterminal position of its horn and in the lateral projection of the anterior rim of its orbit. The zygomatic arch of *Ningxiatherium* is slender, however, and probably plesiomorphic with respect to *Iranotherium*. Probable derived characters of *Ningxiatherium* are a forwards shift of the dentition relative to the orbit [36], the deep narial incision [35], and the ossification of the nasal septum [37]. *Ningxiatherium* is very dolichocephalic, but the polarity of this character is difficult to determine. *Smotherium* and *Elasmotherium* are both markedly brachycephalic, with a single frontal horn base. A synapomorphy of these genera is the strong and branching crista of the upper molars [38]. The premolars are also relatively reduced in size but molarized in both [40]. *Elasmotherium* is the only known rhinocerotoid to develop hypselodont molars [41], and was the last member of the tribe, becoming extinct in the late Pleistocene. *Sinootherium*, on the other hand, lacks good apomorphies.

History and dispersal of elasmotheres

The earliest elasmotheres are represented only by some tiny brachyodont teeth from the lower Miocene Bugti beds of Pakistan, referred by HEISSIG (1972) to *Caementodon*. Rhinocerotini of

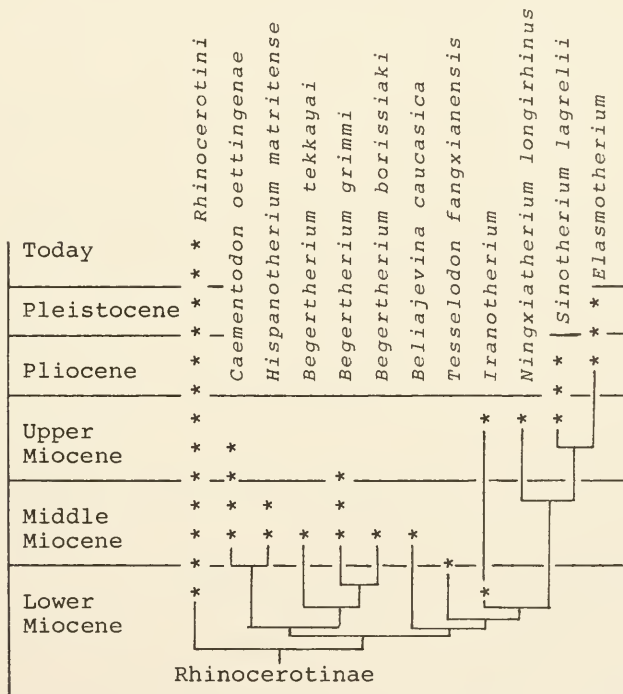


Fig. 2: Historical arrangement of the elasmotherine clades and the outgroup Rhinocerotini. * Real occurrence in the fossil record.

this small size are unknown. This form shows no sign of increasing crown height, but traces of coronal cement are suggestive. The only character in common with *Caementodon oettingenae* from the middle Miocene of the Siwaliks is the lengthening of the metastyle in the upper Molars (FORSTER-COOPER 1934, p. 602, pl. 65, fig. 26, 28–30). This, however, indicates that the *Elasmotherium*-clade, which lacks this derived character, had already split off at that time.

In the middle Miocene the elasmotheres reached their widest range and highest diversity (Fig. 2). The center of origin appears to be Central Asia, but they were also present on the Indian subcontinent as well as in Spain. In the upper Miocene the tribe was mainly restricted to Central and Eastern Asia, with some survivors of *Caementodon* in the Siwaliks and the isolated occurrence of *Kenyatherium* in Africa. In the Plio-Pleistocene their range contracted further, with *Elasmotherium* itself occurring mainly in Central and Northern Asia. Towards the end of their history elasmotheres briefly appeared in Western Europe. DUVERNOY (1855) described a skull fragment of *Elasmotherium* from the Rhine valley as "*Stereoceros galli*".

References

- AGUIRRE, E. & GUÉRIN, C. (1974): Première découverte d'un iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique: *Kenyatherium bishopi* nov. gen, nov. sp. de la formation vallésienne (Miocène supérieur) de Nakali (Kenya). — *Estud. geol.* 30(3): 229–233; Madrid.
- BELAJEVA, E. I. (1971): Über einige Nashörner, Familie Rhinocerotidae aus dem Neogen der westlichen Mongolei (russ.). — *Fauna Mesozoja i Kainozoja zapadnoj Mongolii* 3: 78–97; Moskow.
- BORISSIAK, A. (1935): Neue Materialien zur Phylogenie der Dicerorhinae. — *Dokl. Akad. Nauk. SSSR* 3(8), 8(68): 381–384; Moscow.
- BREUNING, S. (1924): Beiträge zur Stammesgeschichte der Rhinocerotidae. — *Verh. Zool. Bot. Ges. Wien*, 73: 5–45; Wien.
- CHEN, G. (1977): A new genus of Iranotheriinae of Ningxia. — *Vertebr. Palasiatica*, 15: 143–146; Peking.
- CHOW, M. (1958): New elasmotherine rhinoceroses from Shansi. — *Vertebr. Palasiatica*, 2: 135–142; Peking.
- CRUSAFONT, M. & VILLALTA, J. F. (1947): Sobre un interesante Rhinoceros (*Hispanotherium* nov. gen.) del Miocene del valle del Manzanares. — *Las Ciencias*, 12, (4): 869–883; Madrid.
- DUVERNOY, M. (1855): Des espèces de Rhinocéros fossiles... — *Arch. Mus. Hist. Nat.*, 7: 1–104; Paris.
- FISCHER v. WALDHEIM, G. F. (1808): Notice d'un animal fossile de Sibérie inconnu aux naturalistes. — *Progr. invit. sé. publ. Soc. imp. natural.*: 1–28; St. Petersburg.
- FORSTER-COOPER, C. (1934): The extinct rhinoceroses of Baluchistan. — *Philos. Trans. Roy. Soc.*, 123 B: 569–616; London.
- FORTELIUS, M. (1990): Rhinocerotidae from Palar, middle Miocene of Anatolia. — *Journ. human. Evol.*, 19 (in press).
- GROVES, C. P. (1983): Phylogeny of the living species of Rhinoceros. — *Zeitschr. zool. System. Evolutionsf.*, 21, (4): 293–313; Hamburg.
- HEISSIG, K. (1972): Paläontologische und geologische Untersuchungen im Tertiär von Pakistan 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. — *Abh. Bayer. Akad. Wiss., Math.-Naturw. Kl.*, NF 152: 1–112; Munich.
- HEISSIG, K. (1974): Neue Elasmotherini (Rhinocerotidae, Mammalia) aus dem Obermiozän Anatoliens. — *Mitt. Bayer. Staatsslg. Paläont. hist. Geol.*, 14: 21–25; Munich.
- HEISSIG, K., (1976): Rhinocerotidae (Mammalia) aus der Anchitherium-Fauna Anatoliens. — *Geol. Jahrb. Abt. B*, 19: 3–121; Hannover.
- HUANG, X. & YAN, D. (1983): New material of Elasmotherini from Shennongjia, Hubei. — *Vertebr. Palasiatica*, 21, 3: 223–229; Peking.
- KRETZOI, M. (1942): Bemerkungen zu System der nach-miozänen Nashorn-Gattungen. — *Földt. Közl.*, 72: 309–318; Budapest.
- KRETZOI, M. (1943): *Gobitherium* n. g. (Mamm. Rhinoc.). — *Földt. Közl.*, 73: 268–271, Budapest.

- MECQUENEM, DE R. (1908): Contribution à l'étude du gisement des Vertébrés de Maragha et de ses environs. — Délégation en Perse, Ann. D'hist. nat., 1; Paris.
- OSBORN, H. F. (1924): *Serridentinus* and *Baluchitherium* Loh formation, Mongolia. — Am. Mus. Novit., 148: 1–5; New York.
- RINGSTRÖM, T. J. (1923): *Sinotherium lagrelii*, a new fossil Rhinocerotid from Shansi. — Bull. geol. surv. China, 5: 91–94; Peking.
- RINGSTRÖM, T. J. (1924): Nashörner der Hipparion-Fauna Nord-Chinas. — Palaeont. Sinica Ser. C., 1(4): 1–159; Peking.
- THENIUS, E. (1969): Phylogenie der Mammalia, 722 p., Berlin (de Gruyter).
- YAN, D. (1979): Einige fossile miozäne Säugetiere aus dem Kreis Fangxian der Provinz Hupei (chin., germ. summ). — Vert. palasiat., 17(3): 189–199; Peking.